Integrative taxonomy reveals a new species of deep-sea squat lobster (Galatheoidea, Munidopsidae) from cold seeps in the Gulf of Mexico

Paula C. Rodríguez-Flores[1,2], Julie W. Ambler[3], Martha S. Nizinski[1,4]

1　Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, DC 23050, USA

2　Department of Organismic and Evolutionary Biology, Museum of Comparative Zoology, Harvard University, 26 Oxford St., Cambridge, MA 02138, USA

3　Emeritus, Department of Biology, Millersville University, Millersville, PA 17551, USA

4　National Systematics Laboratory, NOAA Fisheries, National Museum of Natural History, Smithsonian Institution, Washington, DC 23050, USA

https://zoobank.org/E15C6ADB-2AB2-4D0C-886F-B2A3AFF3F769

Corresponding author: Paula C. Rodríguez-Flores (rodriguezfloresp@si.edu)

Abstract

The western Atlantic Ocean harbors a diverse fauna of squat lobsters, particularly in the family Munidopsidae. This study introduces *Munidopsis sedna* **sp. nov.**, a species only found in the Gulf of Mexico and the first species reported to be endemic to cold seeps in the western Atlantic. Our investigation incorporates morphological analyses including micro-CT scanning evidence, multilocus molecular phylogeny, and mtDNA phylogeography, as well as ecological data derived from in situ observations and geographic distribution patterns to substantiate the recognition of the new species. Shallow molecular divergences and multiple morphological differences differentiate the new species from its closest relative, *M. longimanus* (A. Milne-Edwards, 1880). Additionally, we explore the potential scenario for ecological speciation within this newly identified taxon and discuss its significance in the context of conservation efforts in the Gulf of Mexico.

Key Words

Introduction

Squat lobsters, an extremely diverse group of anomuran crustaceans, inhabit broad geographic and bathymetric ranges, occurring circumglobally, primarily in tropical and temperate waters, from the surface to abyssal depths (Schnabel et al. 2011). Commonly found in the deep sea at depths greater than 200 m, many species of squat lobsters occur in vulnerable ecosystems in association with hydrothermal vents, cold seeps, and cold-water corals (e.g., Chevaldonné and Olu 1996; Macpherson and Segonzac 2005; Martin and Haney 2005; Baba et al. 2008). The recent increase in deep-sea exploration has led to the discovery of numerous new species. In fact, many new species are discovered and described every year, especially from unexplored areas in the Pacific Ocean (e.g., Baba

2018; Dong et al. 2021; Rodríguez-Flores and Schnabel 2023, Rodríguez-Flores et al. 2023; Macpherson et al. 2024). Renewed interest and recent work in the Caribbean Sea and the Gulf of Mexico has also revealed new species and species complexes in the western Atlantic Ocean (e.g., Vazquez-Bader et al. 2014; Macpherson et al. 2016; Poupin and Corbari 2016; Baba and Wicksten 2017a, 2017b; Coykendall et al. 2017; Rodríguez-Flores et al. 2018, 2022; Gaytán-Caballero et al. 2022).

While systematic research on squat lobsters is active, ecological research on this group is still in its infancy (Coykendall et al. 2017). Few studies have focused on understanding the natural history and ecology of squat lobsters (Lovrich and Thiel 2011). Multiple species of squat lobster are found closely associated with hydrothermal vents and cold seeps, and some species have special

adaptations for living in these habitats (Williams and van Dover 1983; Baba and de Saint Laurent 1992; Baba and Williams 1998; Desbruyères et al. 2006; Gaytán-Caballero et al. 2022). For instance, *Shinkaia crosnieri* Baba & Williams, 1998, cultivates chemosynthetic bacteria on the body setae (Tsuchida et al. 2011; Watsuji et al. 2017). Additionally, several species of *Munidopsis* Whiteaves, 1874 are found occasionally in chemosynthetic environments, taking advantage of high concentrations of available food (Macpherson and Segonzac 2005; Macpherson et al. 2006). Conversely, some other species in the same genus are suggested to be colonists or vagrants (*sensu* Carney 1994) of seeps and hydrothermal vents rather than restricted to living in these kinds of habitats (Carney 1994; Martin and Haney 2005).

However, little is known about squat lobsters utilizing chemosynthetic habitats, particularly those species considered to be endemic (*sensu* Carney 1994). Probably the most studied vent/cold-seep species are the yeti crabs (*Kiwa* Macpherson, Jones & Segonzac, 2005), which have a high dependence on chemosynthetic ecosystems and multiple adaptations to life in these environments (Macpherson et al. 2005; Goffredi et al. 2008; Thatje et al. 2015). As new vent sites and cold seeps are discovered, new squat lobster species living in these habitats are also discovered (Rodríguez-Flores et al. 2023).

Extreme environments such as hydrocarbon seeps, brine pools, and cold-water coral habitats are broadly distributed throughout the Gulf of Mexico (GoM) on the continental slope at depths ranging from 400 to 3,500 m (Cordes et al. 2009). The chemosynthetic communities consist mainly of mussel beds and tube-worm bushes (e.g., *Bathymodiolus* Kenk & Wilson, 1985, and *Lamellibrachia* Webb, 1969, respectively) and have been extensively researched (Carney 1994; Cordes et al. 2007, 2009, 2010; Fisher et al. 2007). The chemosynthetic communities provide habitat for many other invertebrate taxa, such as polynoid polychaetes, trochid gastropods, alvinocarid shrimps, and squat lobsters (Webb 1969; Kenk and Wilson 1985; Roberts et al. 1990; Fisher et al. 2007). For example, squat lobsters in the genus *Munidopsis* have been detected in abundance on tubeworm aggregations and mussel beds associated with these cold seeps (Carney 1994; Bergquist et al. 2003; Lessard-Pilon et al. 2010). Species of *Munidopsis* living there are an important component of the community and rely completely on chemosynthetic production (MacAvoy et al. 2008a, 2008b). Although extensively studied (Bergquist et al. 2003; Cordes et al. 2010; Coykendall et al. 2017), a species of *Munidopsis* frequently found in association with brine pools and cold seeps in the GoM remained unidentified (Fisher et al. 2007; Lessard-Pilon et al. 2010).

Herein, we describe this new species of squat lobster based on molecular and morphological evidence. The new species is morphologically related to *M. longimanus* (A. Milne-Edwards, 1880) and *M. brevimanus* (A. Milne-Edwards, 1880), known from the Gulf of Mexico and the Caribbean. We therefore compare the material of all these species and highlight the morphological characters distinguishing the new taxa from the other species. Additionally, we highlight ecological observations and discuss a potential scenario of ecological speciation with respect to its closely related and co-occurring sympatric congener, *M. longimanus*.

Materials and methods

Ecological data

Specimens of the new species were collected during several cruises conducted in and around chemosynthetic habitats in the northern GoM (see details below in the Material Examined Section). Histograms of depth distribution were done using Past4 Version 4.16 (https://www.nhm.uio.no/english/research/resources/past/) (Hammer et al. 2001). Maps were generated using the free open-source Geographic Information System QGIS Version 3.34.3 (https://qgis.org/en/site/). Layers of chemosynthetic communities and hydrocarbon seeps in the GoM were downloaded from Sinclair and Shedd (2012) (https://www.ncei.noaa.gov/maps/gulf-data-atlas/atlas.htm).

Morphological examination

We examined a total of 103 lots, including 758 specimens deposited in the following collections: Museum of Comparative Zoology (MCZ), Harvard University, Cambridge, MA; Muséum National d'Histoire Naturelle (MNHN), Paris; Benthic Invertebrate Collection at Scripps Institution of Oceanography (SIO-BIC), San Diego, CA; Field Museum of Natural History (FMNH), Chicago, IL; Voss Marine Invertebrate Collections at the University of Miami (UMML), Miami, FL; Texas Cooperative Wildlife Collection (TCWC) at Texas A&M University, College Station, TX; and National Museum of Natural History (USNM), Smithsonian Institution, Washington, DC. The material examined corresponds to the new species and morphologically related species. We used a Leica MZ 12.5 stereomicroscope coupled with a camera lucida to identify, draw, and dissect the squat lobster specimens. Drawings were digitized using a Wacom Intuos Pro tablet with Adobe Illustrator 2024. The terminology used for the species description follows that of Baba et al. (2011). The size of the specimens is indicated by the postorbital carapace length (PCL). The following morphometric features were examined: rostrum length: straight line distance from the base to the distal tip; rostrum width: straight line distance between the lateral limits of the rostral lobe. Measurements of appendages are taken on the dorsal (pereiopod 1), lateral (antennule, pereiopods 2–4), or ventral (antenna) midlines. Measures of the maxillipeds are taken on the extensor margin. Ranges of morphological and meristic variation are included in the description. Abbreviations used in the description are as

follows: **Mxp** = maxilliped; **P1** = pereiopod 1 (cheliped); **P2–4** = pereiopods 2–4 (walking legs 1–3); **M** = male; **F** = female; **ov.** = ovigerous, **m** = meters, **mm** = millimeters. Holotype measurement values are indicated with brackets. Several specimens were selected for DNA extraction, amplification, and sequencing (see below).

Morphological analyses

Several individuals (N = 13) were photographed on the dorsal view using an Olympus Tough Tg-6 digital camera (Suppl. material 1). A scale was included for reference. A combination of anatomical landmarks and semi-landmarks on the carapace, rostrum, and abdomen were used to compare and analyze features of the new species and its closest relative, *M. longimanus* (A. Milne-Edwards, 1880), using the R package geomorph (Adams and Otárola-Castillo 2013). Morphological information (coordinates in axes X and Y) was then transformed into new coordinates (generalized procrustes analyses) and analyzed and visualized using principal component analyses (PCA).

Micro-Computed Tomography (micro-CT)

Two specimens of both the new species and *M. longimanus* were selected for 3D imaging. The specimens were mounted in 15-mL plastic vials and secured using parafilm and synthetic cotton to minimize their movement during the scanning process. The container was sealed with parafilm.

The micro-CT scans were conducted at the MCZ using a SkyScan 1273 scanner (Bruker MicroCT, Kontich, Belgium). The scanner is supplied with a Hamamatsu 130/300 tungsten X-ray source at 40–130 kV and a flat-panel X-ray detector with 6-megapixel (3072 × 1944). The following scanning parameters were chosen: source current=100 µA, source voltage=75 kV, exposure time=1,000 ms, frames averaged=3–4, rotation step = 0.2, frames acquired over 180°=960, filter=no, binning=no, flat field correction=activated. The scanning time ranged from 50 to 140 min. Reconstruction of the cross-section slides was completed using the software NRecon 1.6.6.0, Bruker MicroCT, Kontich, Belgium. To enhance image contrast and compensate for the ring and streak artifacts, the reconstruction parameters were set to the following: smoothing=no, ring artifact correction=5–11, and beam hardening correction=activated. 3D rendering images and segmentation were performed using Amira software (Thermo Fisher Scientific). Images were edited with Photoshop (Adobe).

DNA extraction, amplification, and sequencing

Tissue subsamples used for molecular analyses were taken from the pereiopod 5, which lacks taxonomic value for squat lobsters. However, for smaller specimens or those with detached legs, another pereiopod was used. Although 55 specimens were selected, most failed to yield usable DNA. We amplified the barcode region of the cytochrome *c* oxidase subunit (COI), the mitochondrial 16S ribosomal RNA, and the nuclear 28S ribosomal RNA following the workflow optimized in previous studies on squat lobsters (e.g., Rodríguez-Flores and Schnabel 2023; Rodríguez-Flores et al. 2023). DNA was extracted with the DNeasy Blood and Tissue Kit (Qiagen), according to the manufacturer's protocol. DNA was amplified via PCR using PuReTaq Ready-To-Go (RTG) PCR Beads (Cytiva) with a combination of primers specifically designed for Galatheoidea and Munidopsidae (Rodríguez-Flores et al. 2022) and universal primers (Folmer et al. 1994; Elbrecht and Leese 2017). Specific primers were designed with Geneious Prime 2023.2.1 Build 2023-07020 11:29 (www.geneious.com) from a matrix including only *Munidopsis* spp. and *Galacantha* spp. samples. A portion of the sequences generated for this study were sequenced using a MinION (Oxford Nanopore Technologies, UK), and the rest were outsourced for Sanger sequencing to Genewiz, Cambridge, UK.

After amplification, we pooled the samples in a single PCR product mix (5–10 µL each) for library preparation and Nanopore sequencing following Rodríguez-Flores et al. (2024). The ligation sequencing kit SQK-LSK109 was used for library prep (Oxford Nanopore Technologies, Oxford, UK) following the Amplicons by ligation of Nanopore protocol as well as amplicon sequencing using Nanopore methodology referenced in recent works (e.g., Srivathsan et al. 2021). The NEBNext Ultra kit (New England BioLabs) was used for DNA repair and end-prep (buffer and enzyme) and adaptor ligation (only ligase). A silica bead clean-up was performed first after the end repair and prep step. A second wash took place after adaptor ligation. The washes were done using magnetic beads, AMPure XP, and PCR Purification Reagent (Applied Biosystems) at 0.8× with 70% ethanol. Amplicon sequencing was performed in a MinION using an expired flow cell stored at 4 °C (FLO-MIN106, expired in 2019), which had 246 pores after QC. The run was 36 h long.

Base calling was done with the software Guppy v6.1.7 (Oxford Nanopore), using the super accuracy algorithm. Demultiplexing was done with ONTbarcoder v0.1.9 (Srivathsan et al. 2021), with read coverage set at a minimum of 5 reads.

Molecular phylogenetic analyses

Phylogenetic relationships were estimated based on a concatenated data set of three molecular markers (COI, 16S, and 28S). Following the phylogenies published by Ahyong et al. (2011) and Rodríguez-Flores et al. (2023), we used two related species, *Munidopsis aspera* and *M. robusta*, as outgroups. These species were chosen as

outgroups because they are the closest relatives to the new species that have molecular data publicly available (Rodríguez-Flores et al. 2018, 2023). Details of specimens sequenced and GenBank accession numbers are provided in Table 1. The mean values of uncorrected pairwise genetic distances (p-distances) for the new species and *M. longimanus* were calculated using MEGA11 (Tamura et al. 2021).

We ran BEAST v2.6.3 (Bouckaert et al. 2014) for the Bayesian inference (BI) analyses. We used a partition scheme by gene with linked trees. The nucleotide substitution models were determined using bModelTest, a Bayesian model test package for BEAST 2 (Bouckaert and Drummond 2017). Parameters were set up using BEAUti v2.6.3 (Bouckaert et al. 2014). A strict molecular clock with a clock rate fixed at 1 was used since the time of divergence of the sequences was not estimated. The tree previously selected was a birth-and-death model. Four Markov Chain Monte Carlo (MCMC) runs were conducted for 1×10^7 generations, sampling trees and parameters every 1,000 generations for the estimation of the posterior probabilities. The initial 25% of the generations were discarded as burn-in. The resulting parameter values and convergence of the chains were checked with Tracer v1.7.1 (Rambaut et al. 2018). A maximum credibility tree was built with TreeAnnotator v2.6.3. Phylogenetic trees were plotted and edited in the interactive Tree of Life (iTOL) annotation tool (Letunic and Bork 2019).

Since specimens from two different localities (the Caribbean Sea and GoM; Table 1) were included in the analyses, haplotype networks, using a parsimony network with the function haploNet, were built with the R package pegas (ver. 1.1, see https://cran.r-project.org/package=pegas; Paradis 2010). Analyses were carried out on the COI matrix on a fragment of 503 pb size with no missing data.

Results

Overall, the present results clearly support the existence of a new species of squat lobster in the GoM. The designation of the new species is supported by phylogenetic evidence, morphometric and morphological differences, and marked ecological differences between the new species and its closest relative, *Munidopsis longimanus*. The mean depth of occurrence for the new species is slightly shallower than that of *M. longimanus*, 479–1070 m *versus* 387–1326 m. Additionally, these two species are found in different habitats, with the new species restricted to cold seeps and salt anomalies (Fig. 1), an association not observed for *M. longimanus*.

Geometric, morphometric, and micro-CT results

Selected landmarks and semi-landmarks are illustrated in Fig. 2. We calculated the morphospace of the carapace and abdomen shape using information from the principal components (PCs). PC1 accounted for 40.55% of the variation among the samples, while PC2 accounted for 17.88%. The PCA results indicated two differentiated clusters corresponding to specimens representing two morphotypes: the new species and *M. longimanus*. The morphotype highlighted differences between the two species, including a more elongated

Table 1. Specimens selected for molecular analyses in this study. Locality and GenBank accession numbers are also provided.

Voucher	Species	Locality	CO1	16S	28S
SIO-BIC C13985-1	*Munidopsis sedna* **sp. nov.**	Gulf of Mexico	PP776025	PP777370	PP777379
SIO-BIC C13985-2	*Munidopsis sedna* **sp. nov.**	Gulf of Mexico	PP776026	PP777371	PP777380
SIO-BIC C13985-3	*Munidopsis sedna* **sp. nov.**	Gulf of Mexico	PP776027	PP777372	PP777381
USNM 1407438	*Munidopsis sedna* **sp. nov.**	Gulf of Mexico	PP776028		
USNM 1407440	*Munidopsis sedna* **sp. nov.**	Gulf of Mexico	PP776029		
USNM 1407439	*Munidopsis sedna* **sp. nov.**	Gulf of Mexico	PP776030		
USNM 1666826_3	*Munidopsis sedna* **sp. nov.**	Gulf of Mexico	PP776031		
USNM 1666823_4	*Munidopsis sedna* **sp. nov.**	Gulf of Mexico	PP776032		
USNM 1666826_4	*Munidopsis sedna* **sp. nov.**	Gulf of Mexico	PP776033		
USNM 1666823_3	*Munidopsis sedna* **sp. nov.**	Gulf of Mexico	PP776034		
USNM 1666808_2	*Munidopsis sedna* **sp. nov.**	Gulf of Mexico	PP776035		
USNM 1407437	*Munidopsis sedna* **sp. nov.**	Gulf of Mexico	PP776036		
USNM 1666807_2	*Munidopsis sedna* **sp. nov.**	Gulf of Mexico	PP776037		
MCZ:IZ 48262	*Munidopsis longimanus*	Trinidad and Tobago	PP776038	PP777373	PP777382
ULLZ10851	*Munidopsis longimanus*	Gulf of Mexico	JN166770	JN166741	
MNHN-IU-2013-18823	*Munidopsis longimanus*	Guadeloupe Island	PP776039	PP777374	
MNHN-IU-2013-19045	*Munidopsis longimanus*	Guadeloupe Island	PP776040	PP777375	PP777383
MNHN-IU-2016-6099	*Munidopsis longimanus*	Guadeloupe Island	PP776041	PP777376	PP777384
MNHN-IU-2016-6101	*Munidopsis longimanus*	Guadeloupe Island	PP776042	PP777377	
MNHN-IU-2016-6104	*Munidopsis longimanus*	Guadeloupe Island	PP776043	PP777378	
SIO-BIC C13951	*Munidopsis aspera*	Costa Rica	ON858114	ON858045	ON858114
MNHN-IU-2013-3367/2550	*Munidopsis robusta*	Guadeloupe Island	MG979485	MG979477	ON858171
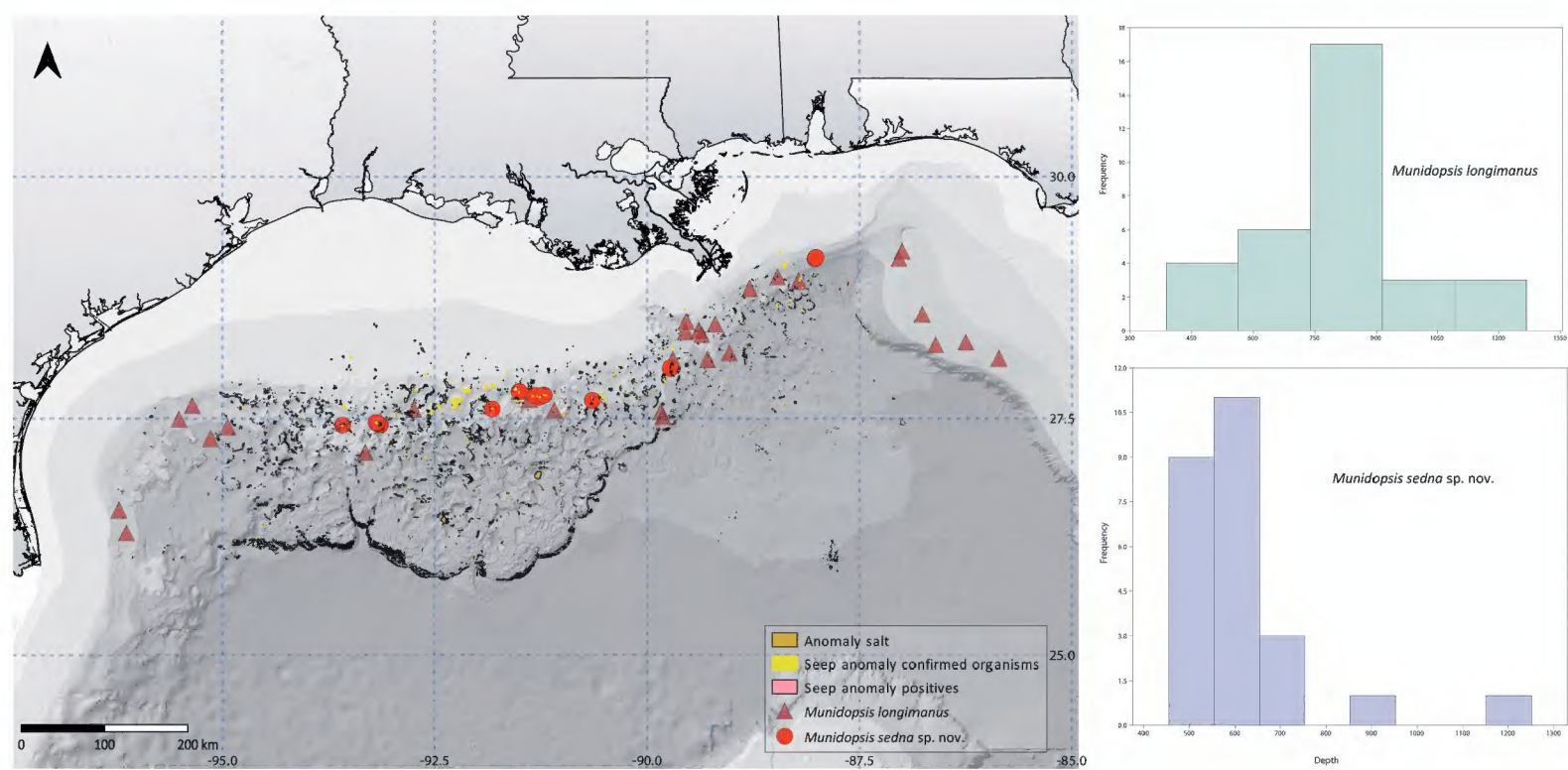
Figure 1. A. Map showing the geographic distribution of the new species and related species in the GoM. The distribution of brine pools and chemosynthetic communities was extracted from Sinclair and Shedd (2012); **B.** Histogram representing the bathymetric distribution of both species.
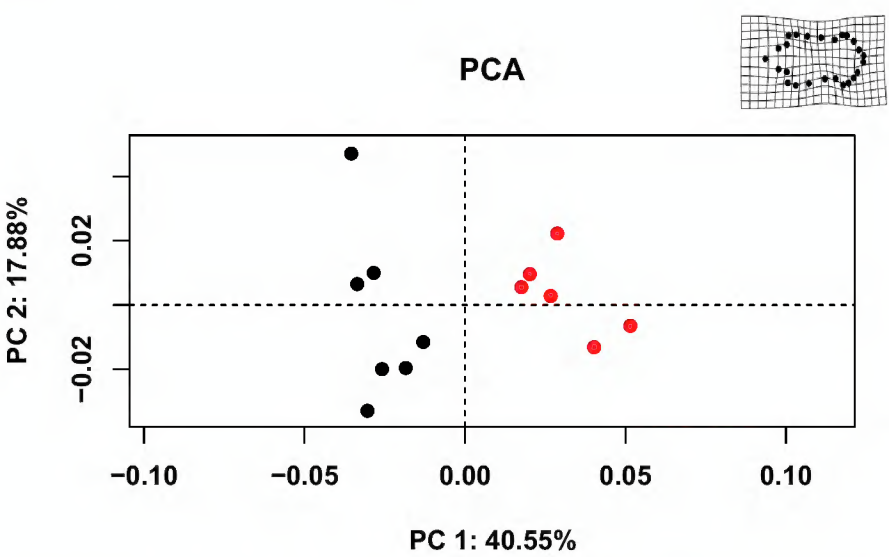

Figure 2. Plot showing PCA results of the analyzed morphospace of both species. Red and black dots represent *Munidopsis sedna* sp. nov. and *Munidopsis longimanus*, respectively.

abdomen for *M. longimanus* and a relatively shorter rostrum for the new species. There was no overlap between the two morphotypes (Fig. 2).

The 3D images resulting from micro-computed tomography showed a clearly distinctive porose tegument with micro-ornamentation in *M. longimanus* that was not present in the new species.

Phylogenetic results

The multilocus BEAST tree recovered two highly supported sister clades (pP = 1) (Fig. 3). The first clade included *Munidopsis longimanus*, occurring in deep waters off Guadalupe, Trinidad and Tobago, and in the GoM.
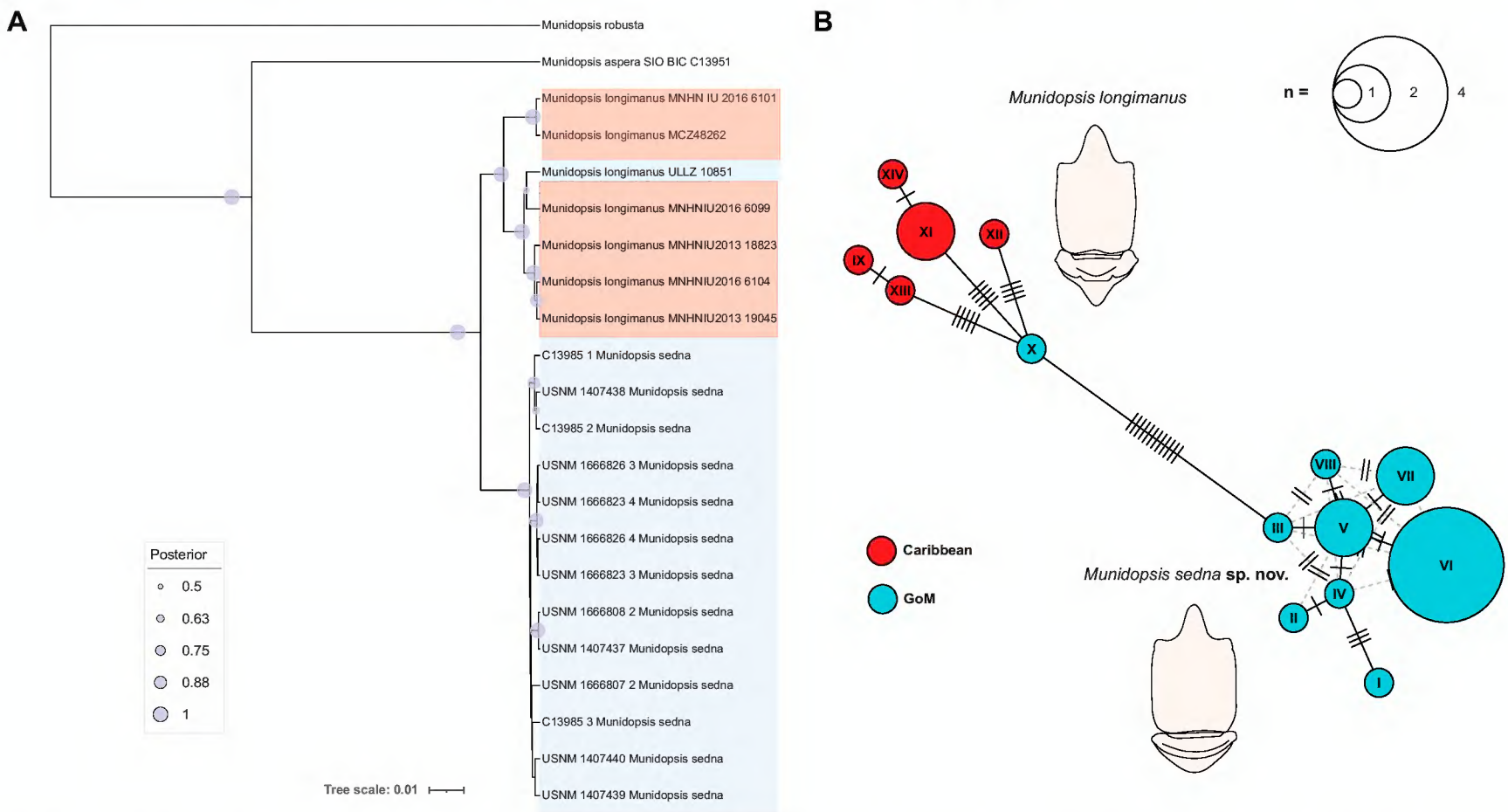
Figure 3. A. Phylogenetic tree resulting from BEAST 2 analyses of the concatenated multilocus matrix (COI, 16S, and 28S). Circles on branches represent the posterior probabilities; **B.** Haplotype network recovered from the analyses of COI data of two species, *Munidopsis longimanus* and *M. sedna* sp. nov. A scale indicates the number of individuals presenting the haplotypes.

The other clade included all specimens of the new species. *Munidopsis aspera* was recovered as a sister species of these two clades; *Munidopsis robusta* was more distantly related. In the COI haplotype network, these two main clades (*M. longimanus* = 6 distinct haplotypes; the new species = 8 distinct haplotypes) are separated by 12 mutational steps. Haplotypes corresponding to *M. longimanus* are grouped in three clusters, all connected by 4–5 mutational steps with the haplotype from the GoM. The network of the new species is represented by a central haplotype connected by 2–3 mutational steps with satellite haplotypes.

The mean genetic p-distances between these two species are 3.25% for the COI, 0.9% for the 16S, and 0.3% for the 28S. Intraspecific mean genetic p-distances were 0.3% for the COI.

Systematics

Superfamily Galatheoidea Samouelle, 1819
Family Munidopsidae Ortmann, 1898
Genus *Munidopsis* Whiteaves, 1874

Munidopsis sedna sp. nov.

https://zoobank.org/5D32B12B-7EC7-495E-A1E8-5BA15E57C8C3
Figs 4, 5, 6A, B, 7

Munidopsis sp. nov. 1: Bergquist et al. (2003), p. 205, 206, 210, 216.
Munidopsis sp.: Fisher et al. (2007), p. 123.
Munidopsis sp. 1: Cordes et al. (2008), p. 781, 783, 786.
Munidopsis sp. (small): Lessard-Pilon et al. (2010), p. 1894, 1885, 1896, 1897.

Material examined. *Holotype.* Gulf of Mexico, United States, Green Canyon, Block 246, 27.6897°N, 90.6450°W, coll. TDI-Brooks International, E. Cordes & C. Fisher, LOPH II, Jason II ROV; Ronald H. Brown R/V, Cruise # RB-10-07, Stn GC 246, sample # MMS-LOPH/II/J2-528/GC246, 17-Oct-2010: M 9.7 mm (USNM 1407437).

Paratypes. Gulf of Mexico, United States, Green Canyon, Block 246, 27.6897°N, 90.6450°W, coll. TDI-Brooks International, E. Cordes & C. Fisher, LOPH II, Jason II ROV; Ronald H. Brown R/V, Cruise # RB-10-07, Stn GC 246, sample # MMS-LOPH/II/J2-528/GC246, 17-Oct-2010: 1 M 7.9 mm (USNM 1407438). —Green Canyon, Block 246, 27.6897°N, 90.6450°W, col. TDI-Brooks International, E. Cordes & C. Fisher, LOPH II Jason II ROV; Ronald H. Brown R/V, Cruise # RB-10-07, Stn GC 246, sample # MMS-LOPH/II/J2-528/GC246, 17-Oct-2010: 1 M 6.9 mm (USNM 1407439) —Green Canyon, Block 246, 27.6897°N, 90.6450°W, coll. TDI-Brooks International, E. Cordes & C. Fisher, LOPH II Jason II ROV; Ronald H. Brown R/V, Cruise # RB-10-07, Stn GC 246, sample # MMS-LOPH/II/J2-528/GC246, 17-Oct-2010: 1 M 8.1 mm (USNM 1407440). —Green Canyon, Block 246, 27.6897°N, 90.6450°W, coll. TDI-Brooks International, E. Cordes & C. Fisher, LOPH II Jason II ROV;

Ronald H. Brown R/V, Cruise # RB-10-07, Stn GC 246, sample # MMS-LOPH/II/J2-528/GC246, 17-Oct-2010: 1 M 4.1 mm, 1 F 2.7 mm (USNM 1407474). —Green Canyon 234 27.7461°N, 91.2211°W, coll. C. Fisher, CHEMO, Seward Johnson II R/V; Johnson Sea Link DSR/V, Cruise # 4436, Stn GC 234, sample # CHEMO/JSL/4436, 534 m, 24-Jun-2002, 1 M 10.3 mm (USNM s). —Green Canyon 234, 27.7461°N, 91.2211°W, coll. C. Fisher, CHEMO, Johnson Sea Link DSR/V, Cruise # 4588, Stn GC 234, sample # CHEMO/JSL/4588 534 m, 5-Sep-2003: 34 M 3.3–9.1 mm, 22 ov. F 4.5–7.6 mm, 17 F 3.6–7.2 mm, 7 specimens with rhizocephalan barnacles parasites (USNM 1666805). —Garden Banks 535, 27.4289°N, 93.5897°W, coll. C. Fisher, CHEMO, Johnson Sea Link DSR/V, Cruise # 4583, Stn GB 535, sample # CHEMO/JSL/4583, 575 m, 3-Sep-2003: 4 M 4.5–7.9 mm, 4 ov. F 5.2–9.4 mm, 3F 4.8–8.0 mm, 1 juv 3 mm (USNM 1666806). Bush Hill, Green Canyon, 27.780300°N, 91.5064°W, col. C. Fisher, CHEMO, Johnson Sea Link I DSR/V; Seward Johnson R/V, Cruise #JSL I 1991, sample # JSL 3129, 549 m, 15-Sep-1991: 1 M 8.5 mm (USNM 1704816).—180 km south of New Orleans, LA, Gulf of Mexico, Brine Pool NR1 cold seep, 27.7230°N, 91.2750°W, coll. R. Vrijenhoek et al., R/V Seward Johnson I and II, 650 m, 3-Oct-2001: 6 M 7.75–10.11 mm, 7 ov. F 6.72–9.9 mm, 1 F 8.91 mm (SIO-BIC C13985).

Other material. For comparison, additional material of *Munidopsis sedna* sp. nov., *M. longimanus*, and *M. brevimanus* (A. Milne-Edwards, 1880) was examined (see Suppl. material 1).

Etymology. In Inuit mythology, *Sedna* is the goddess of the sea and marine animals, also known as the Mother or Mistress of the Sea. The specific name is substantive in apposition.

Diagnosis. Carapace, excluding rostrum as long as broad, dorsal surface nearly smooth or covered with small granules. Rostrum broadly triangular, not acute at tip, *ca.* one-third carapace length. Frontal margin without delimited orbit, transverse. Cervical grooves distinct. Lateral margins subparallel, without distinct spines. Sternum longer than wide, maximum width at sternites 4 to 6; sternite 3 short and wide, width about half that of sternite 4. Abdomen spineless; telson with 10 plates. Eyes small, movable, and unarmed; cornea small, slightly elongated; peduncle larger than cornea. Antennular article 1 swollen laterally. Basal part of each Mxp 3 not separated by an appreciable gap; merus with 2 acute spines on flexor margin. P1 long and slender, more than twice carapace length, longer than P2. P2–4 moderately stout; extensor margin of articles carinate; propodi not expanded distally; dactyli curved distally; flexor margin with row of 8–12 teeth bearing corneous spinules. Epipods absent from all pereiopods.

Description. *Carapace*: As long as broad, widest at posterior part; convex from side to side. Dorsal surface sparsely covered with small granules or nearly smooth, hepatic and anterior branchial areas with minute granules or smooth. Regions well delineated by furrows, anterior and posterior cervical grooves distinct. Gastric region slightly
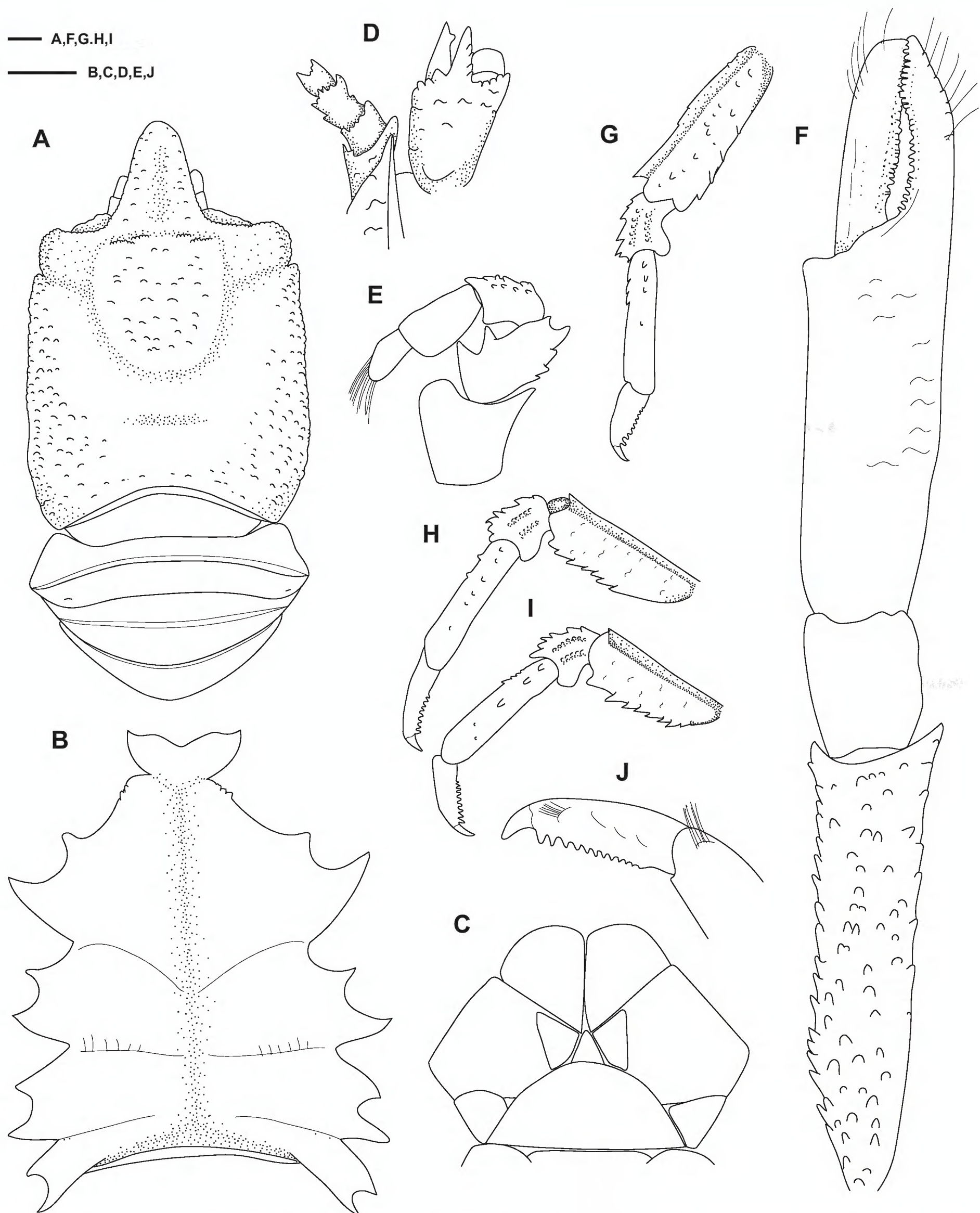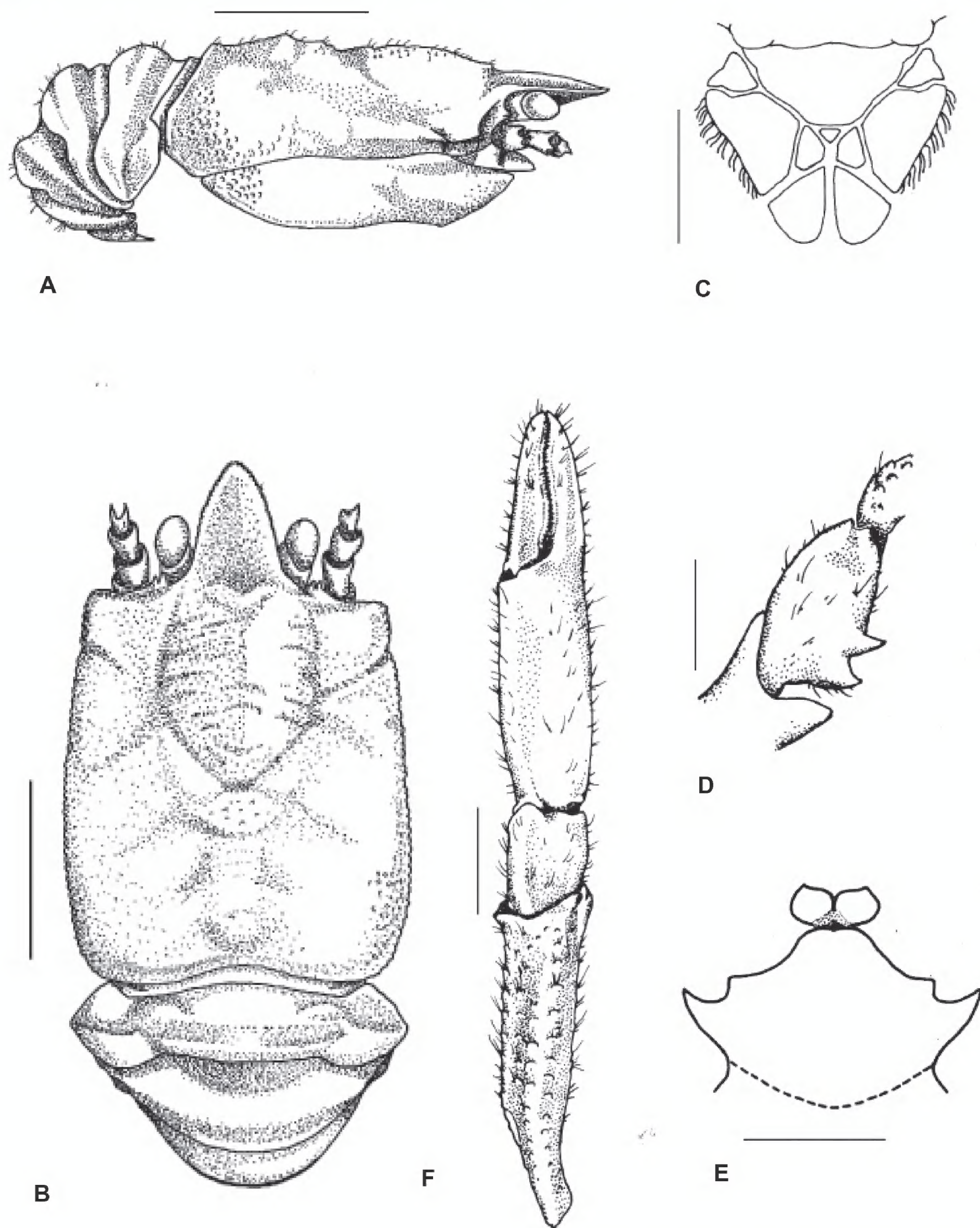
Figure 4. Line drawings of *Munidopsis sedna* sp. nov., Gulf of Mexico, holotype, male 9.7 mm (USNM 1407437). **A.** Carapace and abdomen, dorsal view; **B.** Thoracic sternum, ventral view; **C.** Telson; **D.** Right part of the cephalothorax, ventral view, showing antennular article 1 and antennal peduncle, and anterior part of the pterygostomian flap; **E.** Left Mxp3, lateral view; **F.** Right P1, dorsal view; **G.** Left P2, lateral view; **H.** Left P3, lateral view; **I.** Left P4, lateral view; **J.** Left P2 dactylus, lateral view. Scale bars: 1 mm.

convex. Posterior margin unarmed, dorsally smooth. Rostrum spatulate, horizontally straight, 0.3–[0.4] times carapace length, 0.2–[0.3] times anterior width of carapace, [1.2]–1.9 times as long as wide; dorsal surface concave,

with small granules. Frontal margin straight behind ocular peduncle; outer orbital angle not produced, concave; orbit not delimited. Lateral margins straight, no spines; anterolateral angle not produced; blunt, sparsely granulate;
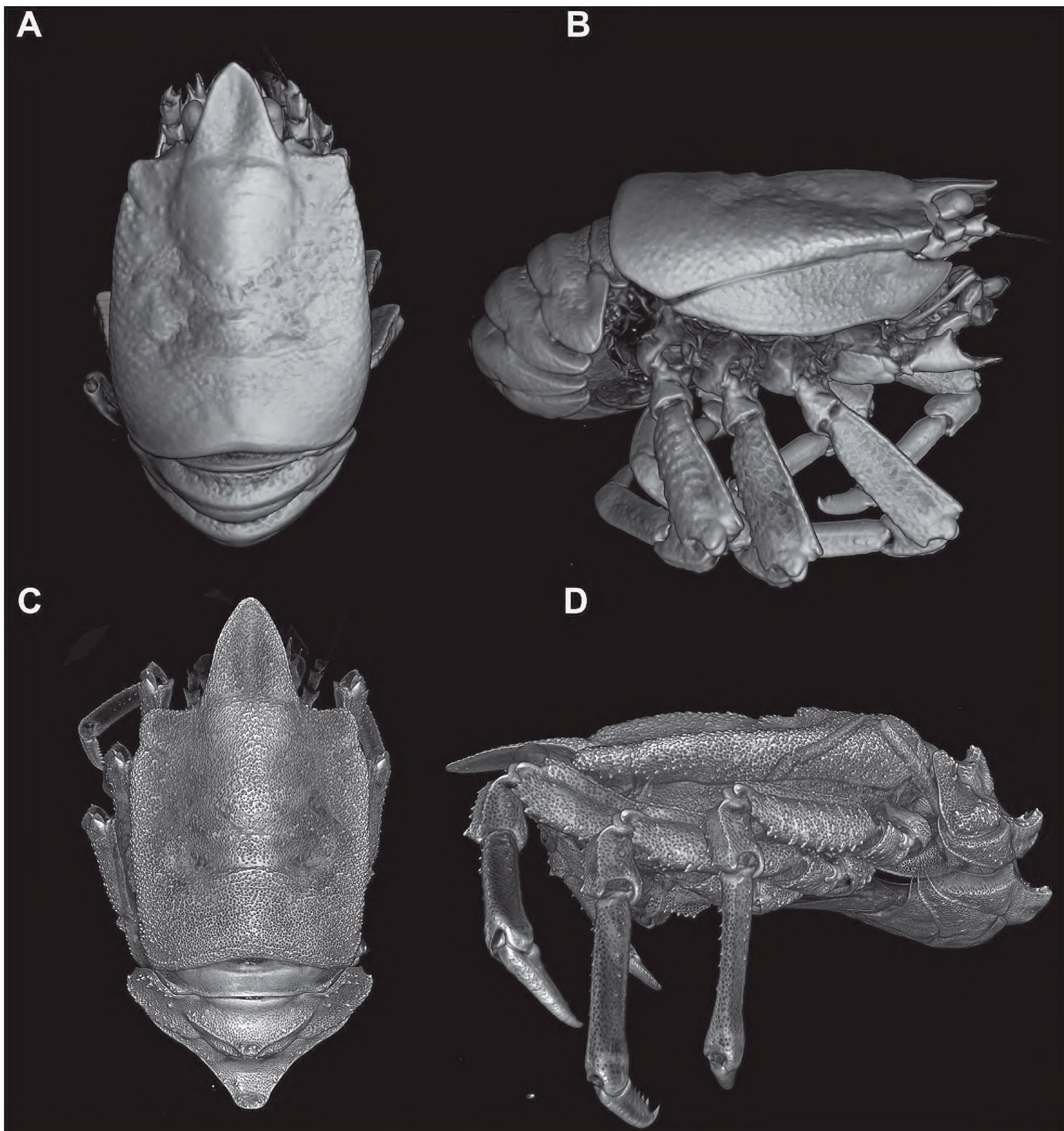
Figure 5. Drawings of *Munidopsis sedna* sp. nov., Gulf of Mexico, paratype, male 8.5 mm (USNM 1704816). **A.** Carapace and abdomen, lateral view; **B.** Carapace and abdomen, dorsal view; **C.** Telson; **D.** Right Mxp3, lateral view; **E.** Sternites 3 and 4, ventral view; **F.** Right P1, dorsal view. Scale bars: 4 mm (**A, B, F**); 2 mm (**C, E**); 1 mm (**D**).

branchial margins granulate; deep notch between hepatic and branchial margins. Epistomial spine absent. Pterygostomian flap surface covered with small granules, anterior margin blunt.

Sternum: Slightly longer than broad, maximum width at sternites 4 to 6. Sternite 3 broad, [3.0] times wider than long, anterolaterally produced and often serrated; anterior margin with broad median notch flanked by 2 lobes.

Figure 6. 3D renderings of micro-computed tomography x-ray images. **A, B.** *Munidopsis sedna* sp. nov., Gulf of Mexico, male, paratype (USNM 1666822); **C, D.** *Munidopsis longimanus*, Guadeloupe (MNHN-2013-18823).

Sternite 4 widely elongate anteriorly; anterior margin often serrated; surface depressed in midline, smooth; greatest width [3.3] times that of sternite 3 and [2.1] times length.

***Abdomen*:** Unarmed. Tergites often with small sparse granules on all surfaces; tergites 2–3 each with 1 elevated transverse ridge; tergites 4–6 without ridges; tergite 6 with weakly developed posterolateral lobes and nearly transverse posteromedian margin. Telson composed of 10 plates; [0.7] times as wide as long.

***Eye*:** Eyestalk movable, partially concealed beneath rostrum; peduncle elongated, smooth, [2.7] times as wide as long; cornea ovoid, narrower than peduncle; length [1.3] times that of peduncle.

***Antennule*:** Article 1 of peduncle with dorsolateral and distolateral spines subequal in size; distolateral margin with denticles; distomesial margin with smaller denticles.

***Antenna*:** Peduncle usually not exceeding eye, armed marginally with denticles and granules. Article 1 with small distolateral spine, distomesial angle produced but unarmed. Article 2 unarmed or with minute distomesial and distolateral spine. Article 3 with small distomesial and distolateral spines or with prominent distal denticles. Article 4 unarmed.

***Mxp3*:** Lateral surface with scattered granules. Ischium [1.1] times longer than merus measured on extensor margin; distal extensor margin serrated. Flexor margin of

Figure 7. In situ image of *Munidopsis sedna* sp. nov. in a brine pool in the Gulf of Mexico. Photo courtesy of the BBC.

merus with 2 prominent proximal spines subequal in size and small distal spine; extensor margin with several denticles and small or large distal spine. Carpus with several denticles on dorsal surface.

P1: Slender, 2.4–2.8 (females) and 3.0–[3.7] (males) times longer than PCL, cylindrical. Merus 3.0–[3.6] times as long as carpus, with denticles and granules. Carpus [1.1]–1.5 times longer than broad, unarmed. Palm unarmed, slender, [2.8]–3.0 times longer than carpus, [2.5]–2.8 times as long as broad. Fingers unarmed, smooth, [0.6] –0.7 times longer than palm; opposable margins nearly straight, gaping, distally spoon-shaped; fixed finger without denticulate carina on distolateral margin. Heterochely present in some specimens.

P2–4: Moderately stout, subcylindrical, flattened in cross-section, slightly decreasing in size posteriorly; surfaces with some denticles and granules. P2 merus moderately slender, [0.7] times PCL, nearly [3.5] times longer than high, [1.3] times length of P2 propodus. Meri decreasing in length posteriorly (P3 merus [0.9] length of P2 merus, P4 merus [0.9] length of P3 merus); extensor margin strongly carinate, distal part ending in thick spine; flexor margin with a row of spines. Carpi with spines on each extensor margin, 2 parallel granulate carinas along dorsal side. Propodi 4.5–5.2 times as long as high, flattened in cross-section, with some tubercles proximally on each extensor margin; lateral surface with some small spines on proximal half; flexor margin unarmed. Dactyli moderately slender, 0.5–0.6 times length of propodi; distal claw short, moderately curved distally; flexor margin nearly straight, armed with 8–12 corneous spines.

Epipods absent from pereiopods.

Eggs: About 5–25 rounded eggs of about 1 mm each.

Coloration: Carapace and abdomen orange, white stripe in midline. Eyes light orange. Pereopods orange or light orange, whitish distally.

Distribution. Gulf of Mexico, from 479 to 1,250 m depth.

Habitat. All specimens examined were collected from cold seeps or associated with the seep communities surrounding brine pools.

Genetic data. COI, 16S rRNA, and 28S rRNA (see Table 1).

Remarks. The new species belongs to the *Elasmonotus* group (A. Milne Edwards, 1880), characterized by species having a carapace with a transverse frontal margin, without a delimited orbit, an elongated cornea, and the dorsal surface of the carapace usually smooth. Within the *Elasmonotus* group, *Munidopsis sedna* sp. nov. is morphologically similar to *M. brevimanus* and *M. longimanus*; however, the new species can be distinguished from these other species by the following morphological characters:

- The abdominal tergites 2–4 are smooth and unarmed in *M. sedna*, whereas they are armed with a broad median spine covered with tubercles in *M. longimanus* and *M. brevimanus*.
- The carapace ornamentation is smooth and/or sparsely granulated in the new species, whereas it is highly tuberculate and porose in *M. brevimanus* and *M. longimanus*, respectively.
- The P1 is longer and more slender in the new species than in *M. brevimanus*.
- The abdomen is more elongated in dorsal view in *M. longimanus* and *M. brevimanus* than in the new species, whereas the rostrum is relatively shorter in the new species.

Mayo (1974) discussed the differences between *M. brevimanus* and *M. longimanus* in detail. The main differences between these two species are the relative length of the

P1, which is much shorter and stouter in *M. brevimanus* than in *M. longimanus* (and also in the new species); and the relative length of the median spines on the abdominal tergites 2–4, which are less projected in *M. brevimanus* than in *M. longimanus* (the spines are absent in the new species). Nevertheless, *M. longimanus* females and juveniles seem to have fewer projected abdominal spines (Mayo 1974; this work). The overlap of morphological characters and the general similarity of these two species led of *M. brevimanus* being considered a junior subjective synonym of *M. longimanus* (see A. Milne-Edwards and Bouvier 1894: 283). However, after further examination of the type specimens of the two species and other material, Chace (1942) resurrected *M. brevimanus* as a valid taxon; this taxonomical decision was later confirmed by Mayo (1974).

Discussion

Squat lobsters from hydrothermal vents: endemic vs. colonizers

Deep-sea chemosynthetic ecosystems, such as hydrothermal vents, cold seeps, and woodfalls, support a variety of organisms, whose association with these ecosystems can vary from vagrant to colonist to endemic members of the benthic community (Carney 1994). Squat lobsters are commonly observed, sometimes in high abundances, in these extreme habitats where they play a key role as heterotrophs consuming chemosynthetic products (e.g., Chevaldonné and Olu 1996; MacDonald et al. 2004; Martin and Haney 2005; Macpherson et al. 2006; Baeza 2011; Gaytán-Caballero et al. 2022). To date, several species from the genera *Munidopsis* and *Munida* have been found in association with these habitats (hydrothermal vents and cold seeps) in the Atlantic, primarily along the Mid-Atlantic ridge, but also associated with cold seeps in the GoM (MacDonald et al. 2004; Macpherson and Segonzac 2005; Macpherson et al. 2006; Coykendall et al. 2017; Gaytán-Caballero et al. 2022). Most species collected from nearby cold seeps are likely vagrants since they have been collected in and around other deep-sea habitats (Wenner 1982; Macpherson and Segonzac 2005; Baba et al. 2008; Coykendall et al. 2017; Gaytán-Caballero et al. 2022). However, *Munidopsis sedna* sp. nov., described herein, is the first species of squat lobster considered to be endemic to cold seep habitats in the GoM in particular and the Atlantic in general.

In the Pacific Ocean, several species are known to be endemic to chemosynthetic habitats, including *Munidopsis alvisca* Williams, 1988 from the East Pacific Rise, *M. lauensis* Baba & de Saint Laurent, 1992 from the Lau Basin, and *M. ryukyuensis* Cubelio, Tsuchida & Watanabe, 2007 from hydrothermal vents in the Hatoma Knoll, and recently discovered species inhabiting cold seeps in the East Pacific (Williams 1988; Baba and de Saint Laurent, 1992; Martin and Haney 2005; Cubelio et al. 2007; Rodríguez-Flores et al. 2023). These endemic species may occur in high abundances and with a certain degree of isolation. For example, *M. lentigo* Williams & Van Dover, 1983, is known only from a few vent sites in the Gulf of California. However, a sister species was discovered recently from vent sites off the Galapagos Islands (Rodríguez-Flores et al. 2023). Given that the geographic distance between these two locations is relatively small, an evolutionary scenario of a recent allopatric speciation process is highly probable. This same scenario could also explain the shallow genetic divergences observed between *M. sedna* sp. nov., currently known only from the northern GoM, and its sister species, *M. longimanus*.

Ecological notes

Based on *in situ* observations and collections, the distribution of *Munidopsis sedna* sp. nov. appears to be restricted to cold seep habitats and brine pools in the northern GOM. This species is a common member of the mobile epifauna associated with chemosynthetic invertebrates that colonize GoM cold seeps on the continental slope (MacDonald et al. 1989, 1990a, 1990b). Specifically, *M. sedna* sp. nov. occurs in and around the structurally complex aggregations of vestimentiferan tube worms (*Lamellibrachia luymesi* and *Seepiophila jonesi*) and mussels (*Bathymodiolus childressi*) that not only provide shelter for the squat lobsters but also are other endemic primary consumers such as non-selective grazers, detritivores, and filter feeders (Bergquist et al. 2003, Fisher et al. 2007, Fig. 5). The new squat lobster can be extremely abundant, occurring at densities on the order of tens per square meter. However, the abundance of the species declines at older stages of the seep community succession (Cordes et al. 2009).

Individuals of *M. sedna* sp. nov. are typically observed clinging to the anterior ends of the vestimentiferan tubes (MacDonald et al. 1989) and occupy a similar niche at mytilid assemblages (Fisher et al. 2007, Fig. 5). These squat lobsters may position themselves on the posterior ends of the tubeworms and mussels to feed on exposed tissue. However, Bergquist et al. (2003) did not observe any significant damage to live vestimentiferans caused by non-lethal plume cropping and suggested that direct predation on live vestimentiferan tissue likely represents a minor trophic contribution at these cold seeps. Additionally, isotope analyses confirmed that the new species did not directly consume *B. childressi* (MacAvoy et al. 2008a). Studies on the trophic ecology of *M. sedna* sp. nov. from cold seeps in Green Canyon and Garden Banks Lease areas (540–640 m) suggest that populations of the species from GoM cold seeps rely heavily on small heterotrophic organisms, which feed on material produced by free-living chemosynthetic bacteria (MacAvoy et al. 2008a, b). Thus, this small squat lobster species acts as an important link among macroinvertebrates, fishes and small heterotrophic organisms that feed on the chemoautotrophic bacteria (MacAvoy et al. 2008a, b; Demopoulos et al. 2010).

Species of *Munidopsis* in the Gulf of Mexico

Munidopsis longimanus, the closest relative and sister species to *M. sedna* sp. nov., is widely distributed throughout the GoM and in the Caribbean Sea at depths ranging from 292 to 1281 m (Mayo 1974; Navas et al. 2003; Felder et al. 2009; Baba et al. 2008; Fig. 1). Given the presumed habitat specificity of *M. sedna* sp. nov. to cold seeps, it is possible that divergent natural selection driven by differences between disparate ecological niches (i.e., ecological speciation) contributes to reproductive isolation. In addition to differences in the distribution patterns and habitat utilization between the two species, molecular evidence, including shallow genetic divergences between lineages and the low interspecific genetic distances presented between the sister species, also supports the hypothesis of ecological speciation. However, it would be necessary to gather more evidence, such as an intensive study of the feeding ecology of *M. longimanus* and a more comprehensive taxonomic sampling of *Munidopsis* species from the western Atlantic, to test this hypothesis. So far, the ecological data of *M. longimanus* is scarce and limited to reports that this species has been collected with *Munidopsis platirostris* (A. Milne-Edwards & Bouvier, 1894), a leptostracan, and the limpet *Notocrater youngi* McLean & Harasewych,1995 (A. Milne-Edwards and Bouvier 1894, McLean and Harasewych,1995; Williams et al. 2019).

Most squat lobster species from the western Atlantic are distributed both in the Caribbean and the GoM, and some also occur in the northwestern and southwestern Atlantic (Baba et al. 2008; Felder et al. 2009; Poupin and Corbari 2016). Only six squat lobster species were exclusively found in the GoM: three *Uroptychus*, one *Munida*, and two *Munidopsis* (Baba et al. 2008; Felder et al. 2009; Baba and Wicksten 2015, 2017a, 2017b; Macpherson et al. 2016). *Munidopsis sedna* sp. nov. here described has been known for several years, but its identity has remained a mystery, probably because of the taxonomic problems posed by two closely related species living in the GoM and the Caribbean, *M. longimanus* and *M. brevimanus*. One of the most conspicuous differences between these two species is the length of the chelipeds (P1), which is shorter in *M. brevimanus*. The length of P1 could be a substantial difference that separates species exploiting different resources, as most galatheids, both deposit feeders and predators, use their P1 to capture food and transfer it to the feeding appendages (Nicol 1932). *Munidopsis brevimanus* is a rare species only known with a few records in the Caribbean and the GoM (Mayo 1974; Navas et al. 2003; Felder et al. 2009), and so far, it has not been found sympatrically with the new species.

Conservation perspective

Cold seep and hydrothermal vent sites, often referred to as "deep islands" of biodiversity, are isolated areas, unstable in time (Vrijenhoek 2010), and are considered vulnerable ecosystems. Given their ephemeral nature and scattered distributions, endemic organisms living in these chemosynthetic habitats show fragmented distributions and isolation, relying on high dispersal capabilities to maintain population connectivity (Vrijenhoek 1997). The fauna endemic to these ecosystems is subject to multiple threats, and if these seeps are massively affected by a catastrophic event (such as a large oil spill), the metapopulation dynamics of organisms associated with this kind of habitat can be severely affected by reducing their possibilities of recolonization, even leading to local or wider geographical-scale complete extinction.

In summary, the new species here presented constitutes a cold-seep endemism only known from a few localities in the GoM. *Munidopsis sedna* sp. nov. has diverged recently from its sister species, which is likely an adaptation to live in the "shallow" cold seeps on the continental shelf in the northern GoM. Its limited distribution pattern and shallow genetic structure suggest stepping-stone dispersal connectivity between nearby cold seeps in the GoM. However, we would need to test this hypothesis with other sources of data, such as rapidly evolving markers that have a resolution at the population scale. This new species is highly vulnerable to extinction threats, given its limited distribution. Therefore, it is critical that we fully characterize and describe the diversity of these fragile deep-sea ecosystems.

Acknowledgments

References

Adams DC, Otárola-Castillo E (2013) Geomorph: An R package for the collection and analysis of geometric morphometric shape data. Methods in Ecology and Evolution 4(4): 393–399. https://doi.org/10.1111/2041-210X.12035

Ahyong ST, Andreakis N, Taylor J (2011) Mitochondrial phylogeny of the deep-sea squat lobsters, Munidopsidae (Galatheoidea). Zo-

ologischer Anzeiger 250(4): 367–377. https://doi.org/10.1016/j.jcz.2011.06.005

Baba K (2018) Chirostylidae of the western and central Pacific: *Uroptychus* and a new genus (Crustacea, Decapoda, Anomura). Tropical Deep-sea Benthos 30. Memoires du Muséum national d'Histoire naturelle 212: 1–612.

Baba K, de Saint Laurent M (1992) Chirostylid and galatheid crustaceans (Decapoda: Anomura) from active thermal vent areas in the southwest Pacific. Scientia Marina 56: 321–332.

Baba K, Wicksten M (2015) *Uroptychus minutus* Benedict, 1902 and a closely related new species (Crustacea, Anomura, Chirostylidae) from the western Atlantic Ocean. Zootaxa 3957(2): 215–225. https://doi.org/10.11646/zootaxa.3957.2.5

Baba K, Wicksten MK (2017a) *Uroptychus atlanticus*, a new species of squat lobster (Crustacea, Decapoda, Anomura, Chirostylidae) from the western Atlantic Ocean. Zootaxa 4227(2): 295–300. https://doi.org/10.11646/zootaxa.4227.2.10

Baba K, Wicksten MK (2017b) *Uroptychus nitidus* (A. Milne-Edwards, 1880) and related species (Crustacea, Decapoda, Anomura, Chirostylidae) from the western Atlantic. Zootaxa 4221(3): 251–290. https://doi.org/10.11646/zootaxa.4221.3.1

Baba K, Williams AB (1998) New Galatheoidea (Crustacea, Decapoda, Anomura) from hydrothermal systems in the West Pacific Ocean Bismarck Archipelago and Okinawa Trough. Zoosystema 20: 143–156.

Baba K, Macpherson E, Poore GCB, Ahyong ST, Bermudez A, Cabezas P, Lin C-W, Nizinski M, Rodrigues C, Schnabel KE (2008) Catalogue of squat lobsters of the world (Crustacea, Decapoda, Anomura families Chirostylidae, Galatheidae and Kiwaidae). Zootaxa 1905(1): 1–220. https://doi.org/10.11646/zootaxa.1905.1.1

Baba K, Ahyong S, Macpherson E (2011) Morphology of marine squat lobsters. In: Poore GCB, Ahyong ST, Taylor J (Eds) The Biology of Squat Lobsters. CSIRO Publishing, Victoria, Australia, 1–37.

Baeza JA (2011) Squat lobsters as symbionts and in chemo–autotrophic environments. In: Poore GCB, Ahyong ST, Taylor J (Eds) The Biology of Squat Lobsters. CSIRO Publishing, Victoria, Australia, 249–270.

Bergquist DC, Ward T, Cordes EE, McNelis T, Howlett S, Kosoff R, Hourdez S, Carney R, Fisher CR (2003) Community structure of vestimentiferan-generated habitat islands from Gulf of Mexico cold seeps. Journal of Experimental Marine Biology and Ecology 289(2): 197–222. https://doi.org/10.1016/S0022-0981(03)00046-7

Bouckaert R, Drummond AJ (2017) bModelTest: Bayesian phylogenetic site model averaging and model comparison. BMC Evolutionary Biology 17.1: 42. https://doi.org/10.1186/s12862-017-0890-6

Bouckaert R, Heled J, Kühnert D, Vaughan T, Wu CH, Xie D, Suchard MA, Rambaut A, Drummond AJ (2014) BEAST 2: A software platform for Bayesian evolutionary analysis. PLoS Computational Biology 10(4): e1003537. https://doi.org/10.1371/journal.pcbi.1003537

Carney RS (1994) Consideration of the oasis analogy for chemosynthetic communities at Gulf of Mexico hydrocarbon vents. Geo-Marine Letters 14(2–3): 149–159. https://doi.org/10.1007/BF01203726

Chace Jr FA (1942) Reports on the scientific results of the Atlantis expeditions to the West Indies, under the joint auspices of the University of Havana and Harvard University. The Anomuran Crustacea I Galatheidea. Torreia 11: 1–106.

Chevaldonné P, Olu K (1996) Occurrence of anomuran crabs (Crustacea: Decapoda) in hydrothermal vent and cold–seep communi-

ties: a review. Proceedings of the Biological Society of Washington 109(2): 286–298.

Cordes EE, Carney SL, Hourdez S, Carney RS, Brooks JM, Fisher CR (2007) Cold seeps of the deep Gulf of Mexico: Community structure and biogeographic comparisons to Atlantic equatorial belt seep communities. Deep-sea Research. Part I, Oceanographic Research Papers 54(4): 637–653. https://doi.org/10.1016/j.dsr.2007.01.001

Cordes EE, McGinley MP, Podowski EL, Becker EL, Lessard-Pilon S, Viada ST, Fisher CR (2008) Coral communities of the deep Gulf of Mexico. Deep-sea Research. Part I, Oceanographic Research Papers 55(6): 777–787. https://doi.org/10.1016/j.dsr.2008.03.005

Cordes EE, Bergquist DC, Fisher CR (2009) Macro–ecology of Gulf of Mexico cold seeps. Annual Review of Marine Science 1(1): 143–168. https://doi.org/10.1146/annurev.marine.010908.163912

Cordes EE, Hourdez S, Roberts HH (2010) Unusual habitats and organisms associated with the cold seeps of the Gulf of Mexico. In: Kiel S (Ed.) The Vent and Seep Biota. Topics in Geobiology 33, Springer, Dordrecht, 315–331. https://doi.org/10.1007/978-90-481-9572-5_10

Coykendall DK, Nizinski MS, Morrison CL (2017) A phylogenetic perspective on diversity of Galatheoidea (*Munida, Munidopsis*) from cold–water coral and cold seep communities in the western North Atlantic Ocean. Deep-sea Research. Part II, Topical Studies in Oceanography 137: 258–272. https://doi.org/10.1016/j.dsr2.2016.08.014

Cubelio SS, Tsuchida S, Watanabe S (2007) New species of *Munidopsis* (Decapoda, Anomura, Galatheidae) from hydrothermal vent in Okinawa Trough and cold seep in Sagami Bay. Crustacean Research 36(0): 1–14. https://doi.org/10.18353/crustacea.36.0_1

Demopoulos AWJ, Gualtieri D, Kovacs K (2010) Food-web structure of seep sediment macrobenthos from the Gulf of Mexico. Deep-sea Research. Part II, Topical Studies in Oceanography 57(21–23): 1972–1981. https://doi.org/10.1016/j.dsr2.2010.05.011

Desbruyères D, Segonzac M, Bright M (2006) Handbook of deep-sea hydrothermal vent fauna, Second completely revised edition, Linz, Denisia, 18?? 544 pp.

Dong D, Gan Z, Li X (2021) Descriptions of eleven new species of squat lobsters (Crustacea, Anomura) from seamounts around the Yap and Mariana Trenches with notes on DNA barcodes and phylogeny. Zoological Journal of the Linnean Society 192(2): 306–355. https://doi.org/10.1093/zoolinnean/zlab003

Elbrecht V, Leese F (2017) Validation and development of COI metabarcoding primers for freshwater macroinvertebrate bioassessment. Frontiers in Environmental Science 5: 11. https://doi.org/10.3389/fenvs.2017.00011

Felder DL, Álvarez F, Goy JW, Lemaitre R (2009) Decapoda (Crustacea) of the Gulf of Mexico, with comments on the Amphionidacea. In: Felder DL, Camp DK (Eds) Gulf of Mexico Origin, Waters, and Biota, Volume?? 1, Biodiversity: College Station, Tex, Texas AM University Press, 1019–1104.

Fisher C, Roberts H, Cordes E, Bernard B (2007) Cold seeps and associated communities of the Gulf of Mexico. Oceanography 20(4): 118–129. https://doi.org/10.5670/oceanog.2007.12

Folmer O, Black M, Hoeh W, Lutz R, Vrijenhoek R (1994) DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. Molecular Marine Biology and Biotechnology 3(5): 294–299.

Gaytán-Caballero A, Escobar-Briones E, Robles R, Macpherson E (2022) *Munidopsis geyeri* and *M. exuta* (Crustacea, Munidopsidae):

A study of two deep-sea, amphi-Atlantic species that co-occur in the southern Gulf of Mexico. Zootaxa 5213(4): 301–335. https://doi.org/10.11646/zootaxa.5213.4.1

Goffredi SK, Jones WJ, Erhlich H, Springer A, Vrijenhoek RC (2008) Epibiotic bacteria associated with the recently discovered Yeti crab, *Kiwa hirsuta*. Environmental Microbiology 10(10): 2623–2634. https://doi.org/10.1111/j.1462-2920.2008.01684.x

Hammer Ø, Harper DAT, Ryan PD (2001) PAST: Paleontological Statistics Software Package for Education and Data Analysis. Palaeontologia Electronica 4(1): 1–9. http://palaeo-electronica.org/2001_1/past/issue1_01.htm

Kenk VC, Wilson BR (1985) A new mussel (Bivalvia, Mytilidae) from hydrothermal vents, in the Galapagos Rift zone. Malacologia 26(1–2): 253–271.

Lessard-Pilon S, Porter MD, Cordes EE, MacDonald I, Fisher CR (2010) Community composition and temporal change at deep Gulf of Mexico cold seeps. Deep-sea Research. Part II, Topical Studies in Oceanography 57(21–23): 1891–1903. https://doi.org/10.1016/j.dsr2.2010.05.012

Letunic I, Bork P (2019) Interactive Tree Of Life (iTOL) v4: Recent updates and new developments. Nucleic Acids Research 47(W1): W256–W259. https://doi.org/10.1093/nar/gkz239

Lovrich GA, Thiel M (2011) Ecology, physiology, feeding and trophic role of squat lobsters. In: Poore GCB, Ahyong ST, Taylor J (Eds) The Biology of Squat Lobsters CSIRO Publishing, Victoria, Australia, 183–222.

MacAvoy SE, Carney RS, Morgan E, Macko SA (2008a) Stable isotope variation among the mussel *Bathymodiolus childressi* and associated heterotrophic fauna at four cold-seep communities in the Gulf of Mexico. Journal of Shellfish Research 27(1): 147–151. https://doi.org/10.2983/0730-8000(2008)27[147:SIVATM]2.0.CO;2

MacAvoy SE, Morgan E, Carney RS, Macko SA (2008b) Chemoautotrophic Production Incorporated by Heterotrophs in Gulf of Mexico Hydrocarbon Seeps: An Examination of Mobile Benthic Predators and Seep Residents. Journal of Shellfish Research 27(1): 153–161. https://doi.org/10.2983/0730-8000(2008)27[153:CPIBHI]2.0.CO;2

MacDonald IR, Boland GS, Baker JS, Brooks JM, Kennicutt MC II, Bidigare RR (1989) Gulf of Mexico chemosynthetic communities II: Spatial distribution of seep organisms and hydrocarbons at Bush Hill. Marine Biology 101: 235–247. https://doi.org/10.1007/BF00391463

MacDonald IR, Guinasso Jr NL, Reilly JF, Brooks JM, Callender WR, Gabrielle SG (1990a) Gulf of Mexico hydrocarbon seep communities: VI Patterns of community structure and habitat. Geo-Marine Letters 10(4): 244–252. https://doi.org/10.1007/BF02431071

MacDonald IR, Reilly JF II, Guinasso Jr NL, Brooks JM, Carney RS, Bryant WA, Bright TJ (1990b) Chemosynthetic mussels at a brine-filled pockmark in the northern. Gulf of Mexico Science 248: 1096–1099. https://doi.org/10.1126/science.248.4959.1096

MacDonald IR, Bohrmann G, Escobar E, Abegg F, Blanchon P, Blinova V, Brückmann W, Drews M, Eisenhauer A, Han X, Heeschen K, Meier F, Mortera C, Naehr T, Orcutt B, Bernard B, Brooks J, De Faragó M (2004) Asphalt volcanism and chemosynthetic life in the Campeche Knolls. Science 304(5673): 999–1002. https://doi.org/10.1126/science.1097154

Macpherson E, Segonzac M (2005) Species of the genus *Munidopsis* (Crustacea, Decapoda, Galatheidae) from the deep Atlantic Ocean, including cold-seep and hydrothermal vent areas. Zootaxa 1095(1): 1–60. https://doi.org/10.11646/zootaxa.1095.1.1

Macpherson E, Jones W, Segonzac M (2005) A new squat lobster family of Galatheoidea (Crustacea, Decapoda, Anomura) from the hydrothermal vents of the Pacific–Antarctic Ridge. Zoosystema 27(4): 709–723.

Macpherson E, Baba K, Segonzac M (2006) Anomura. In: Desbruyères D, Segonzac M, Bright M (Eds) Handbook of deep-sea hydrothermal vent fauna, Second completely revised edition, Linz, Denisia, 434–454.

Macpherson E, Beuck L, Freiwald A (2016) Some species of *Munidopsis* from the Gulf of Mexico, Florida Straits and Caribbean Sea (Decapoda, Munidopsidae), with the description of two new species. Zootaxa 4137(3): 405–416. https://doi.org/10.11646/zootaxa.4137.3.7

Macpherson E, Rodríguez-Flores PC, Machordom A (2024) DNA barcoding and morphology revealed the existence of seven new species of squat lobsters in the family Munididae (Decapoda, Galatheoidea) in the southwestern Pacific. ZooKeys 1188: 91–123. https://doi.org/10.3897/zookeys.1188.114984

Martin JW, Haney TA (2005) Decapod crustaceans from hydrothermal vents and cold seeps: A review through 2005. Zoological Journal of the Linnean Society 145(4): 445–522. https://doi.org/10.1111/j.1096-3642.2005.00178.x

Mayo BS (1974) The systematics and distribution of the deep–sea genus *Munidopsis* (Crustacea, Galatheidae) in the Western Atlantic Ocean. Ph.D. Dissertation, University of Miami, 342 pp.

McLean JH, Harasewych MG (1995) Review of western Atlantic species of cocculinid and pseudococculinid limpets, with descriptions of new species (Gastropoda, Cocculiniformia). Contributions in Science 453: 1–33. https://doi.org/10.5962/p.208088

Milne-Edwards A (1880) Reports on the results of dredging under the supervision of Alexander Agassiz, in the Gulf of Mexico and in the Caribbean Sea,1877, '78, '79, by the U.S Coast Survey Steamer "Blake", Lieut.–Commander C.D Sigsbee, U.S.N, and Commander J.R Bartlett, U.S.N commanding. VIII. Études préliminaires sur les Crustacés. Bulletin of the Museum of Comparative Zoology at Harvard College 8(2): 1–68 [pls1–2].

Milne-Edwards A, Bouvier EL (1894) Considérations générales sur la famille des Galathéidés. Annales des Sciences Naturelles, Zoologie, 7e série 16: 191–327. https://doi.org/10.5962/bhl.title.10042

Navas GR, Bermúdez A, Cruz N, Campos NH (2003) Galatéidos (Decapoda, Anomura, Galattheidae) del Caribe colombiano, incluyendo doce primeros registros. Boletin de Investigaciones Marinas y Costeras 32: 183–218. https://doi.org/10.25268/bimc.invemar.2003.32.0.266

Nicol EA (1932) The feeding habits of the Galatheidea. Journal of the Marine Biological Association of the United Kingdom 18(1): 87–106. https://doi.org/10.1017/S0025315400051316

Paradis E (2010) pegas: An R package for population genetics with an integrated–modular approach. Bioinformatics 26(3): 419–420. https://doi.org/10.1093/bioinformatics/btp696

Poupin J, Corbari L (2016) A preliminary assessment of the deep–sea Decapoda collected during the KARUBENTHOS 2015 Expedition to Guadeloupe Island. Zootaxa 4190(1): 1–107. https://doi.org/10.11646/zootaxa.4190.1.1

Rambaut A, Drummond AJ, Xie D, Baele G, Suchard MA (2018) Posterior summarization in Bayesian phylogenetics using Tracer 1.7. Systematic Biology 67(5): 901–904. https://doi.org/10.1093/sysbio/syy032

Roberts HH, Aharon P, Carney R, Larkin J, Sassen R (1990) Sea floor responses to hydrocarbon seeps, Louisiana continental slope. Geo-Marine Letters 10(4): 232–243. https://doi.org/10.1007/BF02431070

Rodríguez-Flores PC, Schnabel KE (2023) New records and species of deep–sea squat lobsters (Galatheoidea, Munidopsidae) from the Hawaiian Archipelago: An integrative approach using micro-CT and barcodes. PeerJ 11: e14956. https://doi.org/10.7717/peerj.14956

Rodríguez-Flores PC, Macpherson E, Machordom A (2018) Three new species of squat lobsters of the genus *Munidopsis* Whiteaves, 1874, from Guadeloupe Island, Caribbean Sea (Crustacea, Decapoda, Munidopsidae). Zootaxa 4422(4): 569–580. https://doi.org/10.11646/zootaxa.4422.4.7

Rodríguez-Flores PC, Macpherson E, Machordom A (2022) New species of deep–sea squat lobsters (Decapoda, Anomura, Galatheoidea) from Guadeloupe, French West Indies, unveiled through integrative taxonomy. Journal of Crustacean Biology 42(1): 1–14. https://doi.org/10.1093/jcbiol/ruab070

Rodríguez-Flores PC, Seid CA, Rouse GW, Giribet G (2023) Cosmopolitan abyssal lineages? A systematic study of East Pacific deep–sea squat lobsters (Decapoda, Galatheoidea, Munidopsidae). Invertebrate Systematics 37(1): 14–60. https://doi.org/10.1071/IS22030

Rodríguez-Flores PC, Torrado H, Combosch D, Giribet G (2024) Diversity of squat lobsters on coral reefs in Guam, Mariana Islands, with the description of two new species and notes on their natural history. Marine Biodiversity 54(4): 57. https://doi.org/10.1007/s12526-024-01446-4

Schnabel KE, Cabezas P, McCallum A, Macpherson E, Ahyong ST, Baba K (2011) Worldwide distribution patterns of squat lobsters. In: Poore GCB, Ahyong ST, Taylor J (Eds) The Biology of Squat Lobsters. CSIRO Publishing, Victoria, Australia, 149–182.

Sinclair J, Shedd W (2012) Petroleum hydrocarbon seeps in deep waters of the central and western Gulf of Mexico. In: Gulf of Mexico Data Atlas [Internet]Stennis Space Center (MS). National Centers for Environmental Information [1 screen]. https://gulfatlas.noaa.gov

Srivathsan A, Lee L, Katoh K, Hartop E, Kutty SN, Wong J, Yeo D, Meier R (2021) ONTbarcoder and MinION barcodes aid biodiversity discovery and identification by everyone, for everyone. BMC Biology 19(1): 217. https://doi.org/10.1186/s12915-021-01141-x

Tamura K, Stecher G, Kumar S (2021) MEGA11: Molecular evolutionary genetics analysis version 11. Molecular Biology and Evolution 38(7): 3022–3027. https://doi.org/10.1093/molbev/msab120

Thatje S, Marsh L, Roterman CN, Mavrogordato MN, Linse K (2015) Adaptations to hydrothermal vent life in *Kiwa tyleri*, a new species of yeti crab from the East Scotia Ridge, Antarctica. PLoS ONE 10(6): e0127621. https://doi.org/10.1371/journal.pone.0127621

Tsuchida, S, Suzuki, Y, Fujiwara, Y, Kawato, M, Uematsu, K, Yamanaka, T, Mizota C, Yamamoto, H (2011) Epibiotic association between filamentous bacteria and the vent–associated galatheid crab, *Shinkaia crosnieri* (Decapoda, Anomura). Journal of the Marine Biological Association of the United Kingdom 91(1): 23–32. https://doi.org/10.1017/S0025315410001827

Vazquez–Bader AR, Gracia A, Lemaitre R (2014) A new species of *Munidopsis* Whiteaves, 1874 (Crustacea, Anomura, Galatheoidea, Munidopsidae) from the Gulf of Mexico and Caribbean Sea. Zootaxa 3821(3): 354–362. https://doi.org/10.11646/zootaxa.3821.3.4

Vrijenhoek RC (1997) Gene flow and genetic diversity in naturally fragmented metapopulations of deep–sea hydrothermal vent animals. The Journal of Heredity 88(4): 285–293. https://doi.org/10.1093/oxfordjournals.jhered.a023106

Vrijenhoek RC (2010) Genetic diversity and connectivity of deep-sea hydrothermal vent metapopulations. Molecular Ecology 19(20): 4391–4411. https://doi.org/10.1111/j.1365-294X.2010.04789.x

Watsuji TO, Tsubaki R, Chen C, Nagai Y, Nakagawa S, Yamamoto M, Nishiura D, Toyofuku T, Takai K (2017) Cultivation mutualism between a deep-sea vent galatheid crab and its chemosynthetic epibionts. Deep-sea Research. Part I, Oceanographic Research Papers 127: 13–20. https://doi.org/10.1016/j.dsr.2017.04.012

Webb M (1969) *Lamellibrachia barhami*, gen. nov. sp. nov. (Pogonophora), from the Northeast Pacific. Bulletin of Marine Science 19(1): 18–47.

Wenner EL (1982) Notes on the Distribution and Biology of Galatheidae and Chirostylidae (Decapoda, Anomura) from the Middle Atlantic Bight. Journal of Crustacean Biology 2(3): 360–377. https://doi.org/10.2307/1548053

Williams AB (1988) New marine decapod crustaceans from waters influenced by hydrothermal discharge, brine, and hydrocarbon seepage. Fish Bulletin 86: 263–287.

Williams AB, van Dover CL (1983) A new species of *Munidopsis* from submarine thermal vents of the East Pacific Rise at 21°N (Anomura, Galatheidae). Proceedings of the Biological Society of Washington 96(3): 481–488.

Williams JD, Boyko CB, Rice ME, Young CM (2019) A report on two large collections of the squat lobster *Munidopsis platirostris* (Decapoda, Anomura, Munidopsidae) from the Caribbean, with notes on their parasites, associates, and reproduction. Journal of Natural History 53(3–4): 159–169. https://doi.org/10.1080/00222933.2019.1582817

Supplementary material 1

Material examined

Authors: Paula C. Rodríguez-Flores, Julie W. Ambler, Martha S. Nizinski

Data type: xlsx

Link: https://doi.org/10.3897/zse.@@.127169.suppl1